

Effect of fertilization on production of epigeous basidiocarps by mycorrhizal fungi in loblolly pine plantations¹

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Received October 18, 1977

MENGE, J. A., and L. F. GRAND. 1978. Effect of fertilization on production of epigeous basidiocarps by mycorrhizal fungi in loblolly pine plantations. *Can. J. Bot.* **56**: 2357–2362.

Basidiocarps of 39 epigeous species of proven or potential mycorrhizal fungi were found in three fertilized *Pinus taeda* plantations during 1972 and 1973. The largest numbers of basidiocarps on all three plantations were found on nonfertilized plots or plots fertilized with P only. Fewest basidiocarps were found on plots fertilized with N. Numbers of basidiocarps of *Suillus hirtellus* were decreased by N fertilization. Numbers of basidiocarps of some other potential mycorrhizal fungi were not altered substantially by fertilization treatments. The average numbers of total living mycorrhizal tips were correlated well with average numbers of epigeous basidiocarps of proven or potential mycorrhizal fungi on fertilized plots. However, if mycorrhizal tips formed by *Cenococcum geophilum*, which do not form visible basidiocarps, were ignored, the remaining mycorrhizal tips were not well correlated with numbers of basidiocarps of proven or potential mycorrhizal fungi.

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Les auteurs ont trouvé, en 1972 et 1973, les basidiocarpes de 39 espèces de champignons mycorrhizateurs prouvés ou potentiels dans trois plantations de *Pinus taeda* fertilisées. Les nombres les plus élevés de basidiocarpes dans les trois plantations sont apparus dans les parcelles non-fertilisées ou celles fertilisées avec du phosphore seulement. Les plus petits nombres de basidiocarpes proviennent de parcelles fertilisées avec de l'azote. L'abondance des basidiocarpes du *Suillus hirtellus* a été diminuée par la fertilisation azotée. L'abondance des basidiocarpes de d'autres champignons mycorrhizateurs potentiels n'a pas été modifiée de façon marquée par les fertilisants. Les nombres moyens de l'ensemble des extrémités racinaires mycorrhiziennes vivantes sont en corrélation avec les nombres moyens de basidiocarpes épiques de champignons mycorrhizateurs prouvés ou potentiels dans les parcelles fertilisées. Cependant, si on ne considère pas les apex mycorrhiziens formés par le *Cenococcum geophilum*, lequel ne produit pas de basidiocarpes visibles, l'ensemble des apex mycorrhiziens qui restent, ne montre pas une bonne corrélation avec les nombres des basidiocarpes de champignons mycorrhizateurs prouvés ou potentiels.

[Traduit par le journal]

Introduction

Little is known about the effect of forest fertilization on production of basidiocarps by mycorrhizal fungi. Fertilization of forest soils has been reported to increase production of basidiocarps of mycorrhizal fungi (5, 8) although application of 125 kg $\text{NH}_4\text{NO}_3/\text{ha}$ did not do so in a spruce plantation in Sweden (9).

Some researchers doubt that numbers of sporophores produced by mycorrhizal fungi are proportional to the prevalence of mycorrhizal roots (1, 2). However, Laiho (5) found that mycelial connections between basidiocarps and mycorrhizal roots were essential for production of sporophores

by *Paxillus involutus* Batsch ex Fr. He also demonstrated that numbers of mycorrhizae formed by *Paxillus involutus* in forest stands were directly correlated with numbers of basidiocarps of *Paxillus involutus*. In a separate study, the severing of spruce roots inhibited production of sporophores by mycorrhizal fungi (9). Not only was the mycorrhizal association necessary for production of basidiocarps by *Thelephora terrestris* (Ehrh.) Fr., but maturation of the basidiocarps ceased when the host plants were covered with a bag which interfered with photosynthesis (4). Thus, the production of basidiocarps may be a sensitive indicator of the extent of symbiosis, at least for mycorrhizal fungi which fruit regularly.

The purpose of this study was to (1) identify potential epigeous mycorrhizal fungi commonly found in plantations of *Pinus taeda* L. (loblolly pine) in North Carolina; (2) determine the effects of fertilization on production of epigeous sporophores

¹Paper No. 5382 of the Journal Series of the North Carolina Agricultural Experiment Station, Raleigh. This study was supported in part by the North Carolina Forest Fertilization Cooperative.

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TABLE 1. Effect of fertilization on production of epigeous basidiocarps by the most frequently observed, proven or potential mycorrhizal fungi in two 11-year-old *Pinus taeda* plantations in North Carolina. Values given are mean numbers of basidiocarps observed for three replicate 0.0049-ha plots on each of the two plantations

Fungal symbiont	Fertilization treatments per hectare ^a						
	Nonfertilized	56 kg N	112 kg N	25 kg P	25 kg P 56 kg N	25 kg P 112 kg N	25 kg P 112 kg N 56 kg K
<i>Amanita citrina</i>	1.2	1.8	2.5	1.0	1.0	0.8	1.5
<i>A. flavoconia</i>	1.3	0.8	0.0	0.0	0.2	2.3	1.7
<i>A. rubescens</i>	4.8	3.2	0.5	0.7	1.0	1.8	2.7
<i>Cantharellus cibarius</i>	2.0	0.0	0.0	0.0	0.0	1.3	0.0
<i>Chroogomphus rutilus</i>	5.0	0.2	0.0	0.5	0.0	0.5	1.3
<i>Laccaria laccata</i>	0.5	0.0	0.0	3.2	3.0	0.0	0.3
<i>Lactarius piperatus</i>	0.8	0.7	0.2	0.3	0.0	0.7	0.5
<i>L. subdulcis</i>	0.5	1.0	1.3	0.3	1.7	1.3	1.7
<i>L. volemus</i>	0.8	0.2	0.0	1.8	1.8	0.3	0.8
<i>Suillus hirtellus</i> ^b	10.8A	1.8AB	0.2B	11.2A	1.3AB	0.3B	1.5AB
Total ^b	28.0A	9.7B	4.7C	19.0AB	10.0BC	9.5BC	12.0B

^aFertilizers were applied as NH_4NO_3 , $\text{Ca}(\text{H}_2\text{PO}_4)_2$, and KCl.

^bValues in each row not followed by an identical letter were significantly different ($P = 0.05$) as indicated by Duncan's multiple-range test after square root transformation. Basidiocarp numbers not followed by letters were not significantly different ($P = 0.05$) from other observed basidiocarp numbers for the same species.

by proven and potential mycorrhizal fungi; and (3) examine the relationship between numbers of epigeous sporophores of proven and potential mycorrhizal fungi and numbers of mycorrhizal tips in these plantations. Hypogeous mycorrhizal fungi were not included because detection was difficult and would have damaged the study sites.

Materials and Methods

As part of fertilization trials by the North Carolina State University Forest Fertilization Cooperative, seven fertilizer treatments (Table 1) were established in March 1972, in two 11-year-old stands of *P. taeda* (Table 2). Each fertilization treatment (Table 1) was applied to three replicate plots in each stand. The plots, 0.0049 ha in size, were arranged in a randomized block design.

To determine if time of fertilization with N altered epigeous basidiocarp production by mycorrhizal fungi, 336 kg N/ha in the form of NH_4NO_3 was applied to plots on a third plantation of 21-year-old *P. taeda* (Table 2) at different times during the season (Table 3). These treatments were replicated three times on 0.049-ha plots in a randomized block design.

All plots were examined monthly for epigeous basidiocarps of proven or potential mycorrhizal fungi. Genera of fungal species listed as mycorrhizal by Trappe (12), with the exception of *Agaricus*, were considered to be potential mycorrhizal fungi in this study. The 11-year-old loblolly pine stands were examined from March 1972 to December 1973, while the 21-year-old stand was examined from August 1972 (when the last fertilization treatment was applied) to December 1973.

Roots of *P. taeda* were removed from each plot in the two 11-year-old plantations in cylindrical cores of soil at 2-month intervals between April and December during 1972 and 1973. Ten soil cores, 7.5 cm deep $\times$ 1.2 cm diameter (85 cm³), were collected at random from each plot at each sampling period and stored in plastic bags at 4°C. Cores were then placed in 0.5- ℓ wide-mouth jars fitted with 1-mm mesh screen covers (two cores per jar). Cores were soaked in tap water overnight and rinsed

vigorously under running tap water until roots and soil separated. The contents of the jars were swirled and poured onto a 0.147-mm sieve. All roots in each soil sample were recovered by this method. Roots and organic debris were removed from the sieve and the number of living and dead mycorrhizal root tips of mycorrhizae were counted under a binocular microscope ($\times 20$) (7). The total surface area of living mycorrhizal tips of each type was calculated by the method of Lorio *et al.* (6).

Results

Basidiocarps of 39 epigeous species of proven or potential mycorrhizal fungi were found in the three *P. taeda* plantations studied during 1972 and 1973 (Table 4). Among these species, only *Cantharellus cibarius*, *Laccaria laccata*, and *Suillus hirtellus* had been proven to form mycorrhizae with *Pinus taeda* (12, L. F. Grand: unpublished data). The remaining 36 species were considered potential symbionts of *P. taeda* (12). The most common potential mycorrhizal fungi found to be associated with *P. taeda* in both fertilized and nonfertilized plots were *Amanita citrina*, *A. flavoconia*, *A. rubescens*, *Chroogomphus rutilus*, *Lactarius cyathulus*, *L. subdulcis*, and *L. volemus* (Table 4).

Although the average numbers of basidiocarps from each of the two 11-year-old plantations were different, the effects due to fertilization were similar and for this reason data from the two 11-year-old plantations were pooled (Tables 1 and 5). The largest numbers of basidiocarps on all three plantations were found on nonfertilized plots or plots fertilized with P only (Tables 1, 3, and 5). Fewer basidiocarps of proven or potential mycorrhizal fungi were found on plots fertilized with N than on

TABLE 2. Characteristics of the plantations of *Pinus taeda* studied in North Carolina (all values given are based on measurements prior to application of the fertilization treatment)

Characteristic	Plantation located near:		
	Rougemont	Wood	Tillery
Physiographic province	Piedmont	Piedmont	Coastal plain
Age in 1972, years	21	11	11
Spacing, m	2 × 2.3	2 × 2.3	2.3 × 2.3
Site index, m/50 years	25.9	24.4	25.9
Soil texture	Loam	Sandy loam	Sandy loam
Drainage	Good	Good	Poor
Depth of litter, mm	45	23	33
Acidity, pH	5.8	4.8	4.6
Organic matter, %	2.5	3.1	2.9
N in needles ^a			
in March 1972, %	1.21	1.26	1.34
P in needles ^a			
in March 1972, %	0.13	0.11	0.11
Extractable soil minerals, kg/ha ^b			
P	4.4	6.4	3.4
K	172	88	49
Ca	1068	376	328
Mg	188	57	48
Mn	86	68	17

^aFoliage analysis values of less than 1.2% N and 0.10% P indicate a deficiency of these elements according to Fowells and Krauss (3).

^bExtractable soil minerals were determined by the Agronomic Division, Soil Testing Laboratory, North Carolina State Department of Agriculture, Raleigh, NC, by dilute acid extraction.

nonfertilized plots or plots fertilized with P only (Tables 1, 3, and 5).

Basidiocarp production by *Amanita citrina*, *Lactarius piperatus*, and *L. subdulcis* was not inhibited greatly by any of the fertilization treatments (Table 1). Greater numbers of basidiocarps of *Suillus hirtellus* were found on nonfertilized plots and plots fertilized with P, than on plots which were fertilized with 112 kg N/ha or 112 kg N plus 25 kg P/ha.

Except for the NPK treatment, fewer numbers of total mycorrhizal root tips per 100 cm³ of soil were found in plots fertilized with N than in nonfertilized plots or plots fertilized with P only (Table 5). The average numbers of living mycorrhizal tips per 100 cm³ of soil were correlated ($r = 0.88$, $P = 0.01$) with average numbers of epigeous basidiocarps of proven and potential mycorrhizal fungi on plots that received similar treatments (Table 5). Mycorrhizal tips and epigeous basidiocarp numbers were not correlated within individual plots ($r = 0.01$), however. Furthermore, after mycorrhizae formed by *Cenococcum geophilum* Fr. (Syn. *Cenococcum graniforme* (Sow.) Ferd. and Winge) were removed from the total number of mycorrhizal tips (since this fungus does not produce visible sporophores in nature (11)), the remaining living mycorrhizal tips

TABLE 3. Effect of time of application of NH₄NO₃ on production of epigeous basidiocarps by mycorrhizal fungi in a 21-year-old *Pinus taeda* plantation in North Carolina. Values are mean numbers of basidiocarps from three replicate 0.049-ha plots^a

Time of application of 336 kg of N/ha (as NH ₄ NO ₃)	Average number of basidiocarps per plot	
	Proven and potential mycorrhizal fungi ^a	Proven <i>Pinus taeda</i> mycorrhizal fungi
Nonfertilized	40.3A	32.3A
Winter		
20 Nov. 1971	7.0B	0.0B
Spring		
1 March 1972	4.7B	0.0B
Late spring		
1 June 1972	10.3B	0.3B
Summer		
7 August 1972	0.0B	0.0B
Treatment with 84 kg at each date above	0.0B	0.0B

^aValues in each column not followed by an identical letter are significantly different ($P = 0.05$) as indicated by Duncan's multiple-range test.

were not well correlated ($r = 0.56$) with epigeous basidiocarp numbers on plots that received similar treatments. Similarly, surface area of total mycorrhizae minus mycorrhizae formed by *C. geophilum*

TABLE 4. Proven and potential mycorrhizal fungi observed in both fertilized and non-fertilized plots in three plantations of *Pinus taeda* in North Carolina during 1972 and 1973. Values given are totals for two 11-year-old plantations which were examined monthly from March 1972 to December 1973 and a 21-year-old plantation which was examined monthly from August 1972 to December 1973

Proven ^a and potential mycorrhizal fungi	Total number of basidiocarps ^b observed	% observation periods in which basidiocarps were found ^c	% plots on which basidiocarps were observed ^d
<i>Amanita chlorinosma</i> (Austin) Lloyd	7	7	8
<i>A. citrina</i> (Schaeff.) S. F. Gray	82	15	42
<i>A. brunnescens</i> Atk.	1	1	2
<i>A. bisporigera</i> Atk.	6	1	3
<i>A. flavoconia</i> Atk.	39	5	17
<i>A. magnivelaris</i> Pk.	7	1	2
<i>A. rubescens</i> (Pers. ex. Fr.) S. F. Gray	111	13	42
<i>A. solitaria</i> Fr.	7	7	8
<i>A. vaginata</i> (Fr.) Vitt.	1	1	2
<i>A. verna</i> Fr.	2	3	3
<i>Boletus</i> sp.	2	1	3
<i>Boletellus chrysenteroides</i> (Snell) Sing.	5	1	3
* <i>Cantharellus cibarius</i> Fr.	36	3	7
<i>C. cinnabarinus</i> Schw.	50	1	1
<i>Chroogomphus rutilus</i> (Fr.) O. K. Miller	47	5	13
<i>Cortinarius</i> sp.	13	3	3
<i>Inocybe</i> sp.	4	3	2
* <i>Laccaria laccata</i> (Fr.) Berk. & Br.	44	3	10
<i>L. ochropurpurea</i> (Berk.) Pk.	4	1	3
<i>Lactarius</i> sp.	11	7	7
<i>L. cyathulus</i> Fr.	67	3	13
<i>L. piperatus</i> (L. ex. Fr.) S. F. Gray	42	4	22
<i>L. subdulcis</i> (Bull. ex. Fr.) S. F. Gray	82	5	25
<i>L. theiogalus</i> Fr.	5	2	5
<i>L. volemus</i> Fr.	50	8	27
<i>Lepiota</i> sp.	2	1	2
<i>Lepista caespitosa</i> (Bres.) Sing.	1	1	2
<i>Phylloporus rhodoxanthus</i> (Schw.) Bres.	4	4	7
<i>Russula</i> sp.	3	3	5
<i>R. albida</i> Pk.	11	3	7
<i>R. foetens</i> Fr.	14	5	13
<i>R. fragilis</i> Fr.	4	3	3
<i>Russula uncialis</i> Pk.	3	3	3
<i>R. virescens</i> Fr.	7	4	7
<i>Strobilomyces floccopus</i> (Fr.) Karst.	2	1	3
<i>Suillus decepiens</i> (Berk. & Curt) Smith & Thiers	6	1	2
* <i>S. hirtellus</i> (Pk.) Kuntze	268	15	28
<i>Tylopilus plumbeoviolaceus</i> (Snell & Dick) Sing.	1	1	2
<i>Xerocomus</i> sp.	1	1	2

^aAsterisks indicate proven mycorrhizal fungi.

^bTotal number of sporophores observed on all plots at all observation periods.

^cTotal number of observation periods was 75.

^dTotal number of plots was 60.

was not well correlated with numbers of epigeous basidiocarps of potential or proven mycorrhizal fungi ($r = 0.22$) (Table 5).

Application of NH_4NO_3 , regardless of when it was applied, always significantly reduced production of basidiocarps by proven or potential mycorrhizal fungi (Table 3). However, variation in numbers of basidiocarps observed was so great no

statistically significant effect of time of N application on sporophore production could be demonstrated.

Discussion

Soil nutrient imbalances have frequently resulted in a decrease in mycorrhizal abundance (8, 10). Heavy N fertilization, in particular, can result in

TABLE 5. Relationship between numbers of epigeous basidiocarps of proven and potential mycorrhizal fungi and numbers of mycorrhizal tips on fertilized and nonfertilized plots in two 11-year-old plantations of *Pinus taeda* in North Carolina. Values are means from six 0.0049-ha plots^a

Fertilizer treatments, per ha ^b	Average number of epigeous basidiocarps per plot		Average number of living mycorrhizal tips/100 cm ³ soil		Surface area mycorrhizae (mm ²)/100 cm ³ soil (total mycorrhizae minus mycorrhizae formed by <i>C. geophilum</i>) ^d
	Proven and potential mycorrhizal fungi ^c	Proven <i>P. taeda</i> mycorrhizal fungi	Total mycorrhizal tips	Total mycorrhizal tips minus mycorrhizal tips formed by <i>C. geophilum</i> ^d	
Nonfertilized	36A	13A	1018A	831A	1286A
56 kg N	12C	3B	819C	678B	1112A
112 kg N	6C	0B	872BC	707B	1203A
25 kg P	30AB	14A	1004A	681B	1071A
25 kg P					
56 kg N	18BC	6B	879BC	636B	1079A
25 kg P					
112 kg N	11C	1B	862BC	665B	1067A
25 kg P					
112 kg N					
56 kg K	14C	2B	935AB	726B	1241A

^aValues in each column not followed by an identical letter are significantly different ($P = 0.05$) as indicated by Duncan's multiple-range test. Significant differences between means of basidiocarp numbers of proven *P. taeda* mycorrhizal fungi were obtained after square root transformation.

^bFertilizers were applied as NH_4NO_3 , $\text{Ca}(\text{H}_2\text{PO}_4)_2$, and KCl.

^cPotential mycorrhizal fungi are those genera designated as mycorrhizal by Trappe (12).

^d*Cenococcum geophilum* does not form epigeous sporophores in nature (11).

fewer mycorrhizal tips (7, 8, 10). In this study, the addition of N resulted in fewer mycorrhizal tips and basidiocarps of mycorrhizal fungi. Although addition of a moderate amount of N may restore the nutrient balance to some N-deficient soils and has been reported to stimulate basidiocarp production by *Paxillus involutus* (5), no such effect was observed on the fungi in this study. Instead, the suppressive effect of nitrogen fertilization on epigeous basidiocarp production by proven or potential mycorrhizal fungi appeared to be a rather uniform phenomenon in plantations of *P. taeda* in North Carolina. However, none of the plantations in this study exhibited symptoms of extreme N or P deficiency (Table 2). These data suggest the need for caution in the use of generalizations about the effect of N or other fertilizer treatments upon basidiocarp production by all species of mycorrhizal fungi.

Inhibition of basidiocarp production by proven or potential mycorrhizal fungi could result from the effect of soil factors directly on mycorrhizal fungi. A second alternative is that other soil organisms which are influenced by fertilization could in turn prevent formation of basidiocarps by mycorrhizal fungi. Basidiocarp production by mycorrhizal fungi could also be dependent on the physiology of the symbiotic relationship (4, 5, 9). Slankis (10) indi-

cated that high concentrations of N may disrupt the mycorrhizal relationship by inhibiting auxin production by the fungal symbiont or by becoming assimilated into fungitoxic compounds in the host root. Such a disruption of the mycorrhizal relationship could explain both the smaller numbers of mycorrhizal tips and basidiocarps of mycorrhizal fungi in plots fertilized with N. It appears that both production of basidiocarps and abundance of mycorrhizal tips were regulated by the same factor(s) which was (were) in turn influenced by fertilization. Any of the physiological or edaphic factors described above could influence both numbers of mycorrhizal tips and production of basidiocarps in a similar manner by disrupting the symbiotic relationship.

The poor correlation between numbers of mycorrhizal tips minus mycorrhizal tips formed by *C. geophilum*, which does not produce epigeous sporocarps, and numbers of epigeous basidiocarps of potential and proven mycorrhizal fungi (Table 5) suggests that numbers of mycorrhizae or surface area of mycorrhizae are not the primary factors responsible for the production of basidiocarps by mycorrhizal fungi. These results are consistent with suggestions by Bowen (1) and Bryan and Zak (2) that sporophore production by mycorrhizal fungi does not necessarily reflect the frequency of

these species as symbionts in mycorrhizae since many mycorrhizal fungi fruit sparingly or not at all.

Although evidence has been presented in this study indicating that a direct relationship does not exist between numbers of mycorrhizal tips and numbers of epigeous basidiocarps of mycorrhizal fungi, it does not conclusively rule out the possibility of such a relationship for many fungi. Results of this study are based on total counts of many dissimilar fungi and certainly for individual fungi a direct relationship, such as that reported by Laiho (5), could exist between numbers of mycorrhizal tips and numbers of basidiocarps produced. Since none of the mycorrhizal fungi in this study were positively shown to be involved in mycorrhizal associations with *P. taeda*, some sporophores of nonmycorrhizal fungi may have been inadvertently included in the basidiocarp counts. This could have masked a relationship between numbers of mycorrhizal tips and numbers of basidiocarps. If mycorrhizal fungi which produce hypogeous or otherwise inconspicuous basidiocarps were present in this study, an underestimate of numbers of basidiocarps of mycorrhizal fungi may have occurred.

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